

7. *On a New South African Species of Balanoglossus and a Comparison between it and Balanoglossus capensis (Gilchrist).* By C. J. VAN DER HORST, University of the Witwatersrand.

(With 19 Text-figures.)

IN July 1936 Professor T. A. Stephenson of the University of Cape Town collected some Enteropneusta near Port Elizabeth and sent them to me for identification. The three specimens proved to belong to the genus *Balanoglossus*, two species of which have been described from the S. African coast by Gilchrist, viz. *B. natalensis* and *B. capensis*. The latter species, the anatomy of which has been described in more detail by von Bonde, occurs in a sexual and an asexual generation, known as *B. capensis* and *B. proliferans* (Gilchrist). *B. natalensis* is a large animal, as yet very imperfectly known, but as I collected some material at Delagoa Bay I hope to give a more accurate description of its anatomy soon. The Port Elizabeth specimens are, however, very small, and as *B. capensis* also belongs to the smaller species of this genus an accurate comparison of these specimens with *B. capensis* is necessary. This comparison reveals that the specimens from Port Elizabeth differ in several of their characters from *B. capensis* as well as from all other species of *Balanoglossus*; *B. australiensis* (Hill), however, seems to resemble them most closely. For this reason I am describing the specimens collected by Professor Stephenson as a new species, and have pleasure in naming it

*Balanoglossus stephensoni* n. sp.

*B. stephensoni* was found underneath stones rather close inshore, half buried in muddy sand. For a species of *Balanoglossus* it is remarkable that it lives under stones; this is the usual habitat of *Ptychodera* rather than *Balanoglossus*. Hill mentions that *B. australiensis* is found in loose gravelly sand, especially under and around larger stones, but otherwise the different species of *Balanoglossus* make burrows in the sand more or less U-shaped, as described by Stiasny. According to von Bonde *B. capensis* also occurs generally in coarse sand or gravel.

This species belongs to the smallest among Enteropneusts, and it is undoubtedly the smallest species of *Balanoglossus*. The total length of the specimen of fig. 1 is 38 mm. and of that of fig. 2 only 31.5 mm. *B. proterogonius*, the next largest in size, is about 9 cm. long and *B. australiensis* 10 cm. Even allowing for a considerable contraction in fixing, the living animal will have a total length of well under 10 cm., probably not more than 5 or 6 cm.

In some species of *Balanoglossus*, as, for instance, *B. numeensis*, the proboscis is greatly reduced in size, whereas the collar is long; but a long, well-developed proboscis may also occur in this genus. In *B. stephensoni*, as far as this can be judged from its contracted stage, the proboscis is of a medium size and the collar is rather short for this genus. As the dimensions of these parts depend largely on the degree of contraction in preserved material, they are not of great importance and may be gauged from figs. 1 and 2.

The anterior part of the collar, as frequently occurs in preserved specimens, is undulated. The five epidermal zones, though present, cannot be seen externally except for the narrow ring along the posterior end of the collar, but even this ring zone cannot always be easily distinguished from the part in front of it.

The branchio-genital region is 11–14 mm. long, of which no more than 3 mm. comprises the branchial region proper, so that this region is extremely short. The genital wings are demarcated from the body by a lateral groove (figs. 2 and 13). The posterior end of the collar is directly continuous with the genital wings. This, combined with the fact that the two wings adhered to each other along their free edge by the much swollen epidermis, made it very difficult to expose the branchial region. They also completely covered the anterior liver saccules. The wings are broadest near the posterior end of the branchial region, but on the whole, taking their entire length into consideration, there is not much variation in their breadth as far as the liver region. But in the anterior part of the liver region the wings decrease in size rather abruptly, soon disappearing altogether. In this respect this species obviously differs from *B. capensis*, in which species, as has been figured by von Bonde, the wings decrease very gradually in size from the posterior end of the branchial region, where they reach their maximum breadth. They extend far into the liver region, but as their disappearance is so gradual it is difficult to ascertain their posterior limit. But even more pronounced is the difference between *B. stephensoni* and such species as *B. biminiensis*, where the genital wings end suddenly in

front of the liver region, so that there is a transitional zone between the genital and the liver region.

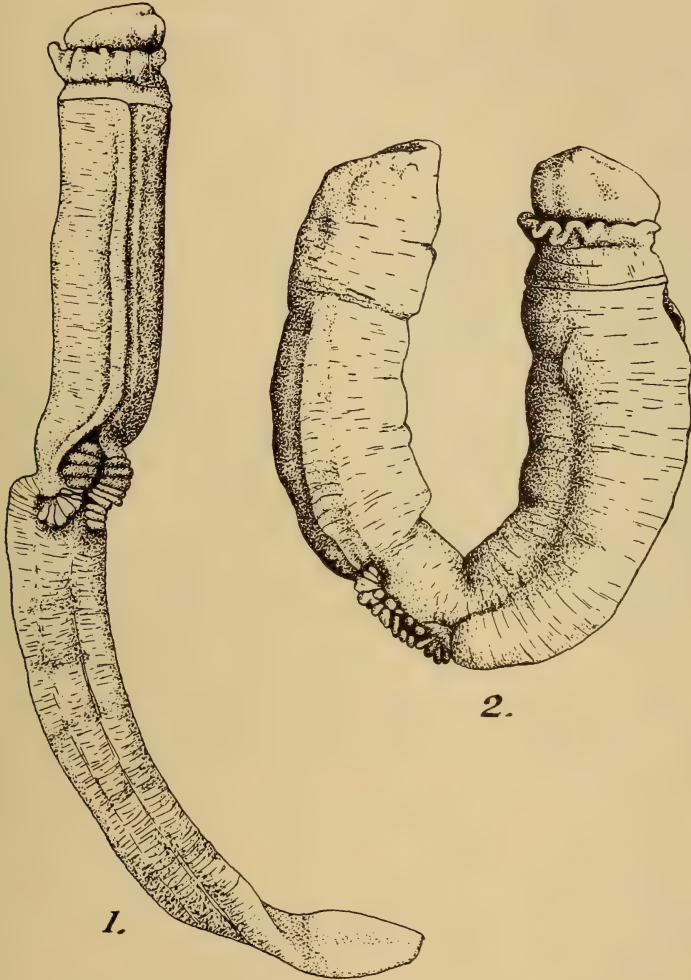


FIG. 1.—*Balanoglossus stephensoni*. Dorsal view.  $\times 4$ .  
FIG. 2.—*Balanoglossus stephensoni*. Side view.  $\times 4$ .

The most obvious external character of *B. stephensoni* is the shortness of the liver region and the abrupt beginning and ending of the external liver saccules. Internally a few more small saccules can be seen both at the anterior and the posterior end of the row, but these do not bulge out on the dorsal surface. In a specimen of

*B. capensis*, 13 cm. long, the liver region measures about 3·5 cm., but as the saccules fade away very gradually at the posterior end it is difficult to give the exact length of the liver region. In Hill's figure of *B. australiensis* the liver region is about one-fifth of the total length of the animal, and in this species also the saccules fade away at the posterior end of the row. In *B. stephensoni*, on the other hand, the liver region comprises only about one-tenth of the total length, but as all three specimens were abruptly bent in the liver region it is difficult to determine the measurements exactly. The number of saccules is accordingly small; there are 20 to 22 in a row, whereas in *B. capensis* about 75 liver saccules are visible in each row.

In both species a few of the liver saccules—4 to 5 in *B. stephensoni*—have a dark brown colour, whereas those in front and behind are pure white. In general two kinds of liver saccules may be distinguished in the Ptychoderidae, but in other species of this family all the frontal saccules differ in colour from the caudal ones, whereas in *B. capensis* and *B. stephensoni* it is only a few in the middle of the row that exhibit this colour variation. This also corresponds with the observations on their histological structure.

The long abdominal region—2 cm. in the specimen of 38 mm.—is characterised by the usual absence of distinguishing features. The caudal region, 3·5 mm. in length, is not swollen, but differs from the abdominal region in the absence or scarcity of the cross-striations.

The preserved specimens are of a uniform white colour, except for the few darker liver saccules. Professor Stephenson informs me that the animals, when alive, had almost the same colour, being rather more yellow.

#### *Internal Anatomy.*

*Proboscis.*—The epidermis and musculature of the proboscis do not show any features that might separate *B. stephensoni* from other species. Von Bonde has described these tissues fully in *B. capensis*.

Concerning the ventral proboscis septum of *B. capensis*, my observations do not quite agree with von Bonde's description. I find this septum greatly reduced in this species. Starting a short distance behind the top of the stomochord there is a thin layer of dorso-ventral muscle fibres just where the septum is to be expected, but no septum in the form of a limiting membrane is visible here. Somewhat more caudally a thick blood-vessel, the ventral proboscis artery, runs from the ventral side of the stomochord to the epidermis, accompanied by some muscle fibres (fig. 10), and more caudally there

are some more but thinner blood-vessels, without, however, any trace of a septum. It is only at the level of the ventral pouch of the stomochord that the septum appears, separating the two ventral coelomic blind-sacs; but here too it is not complete, as there is a large hole in it (fig. 3). Nevertheless the septum extends to the caudal end of the blind-sacs, which are not, however, deep, as they cease at the front end of the skeleton.

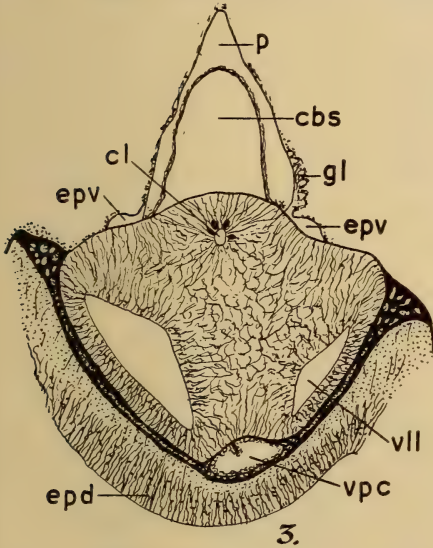


FIG. 3.—*Balanoglossus capensis*. Cross-section of the proboscis organs.  $\times 66$ . *cbs*=central blood space; *cl*=central lumen of stomochord; *epd*=epidermis; *epv*=efferent proboscis vessels; *gl*=caudal end of glomerulus; *p*=pericardium; *vll*=ventro-lateral cavity of stomochord; *vpc*=ventral proboscis coelomic blind-sac.

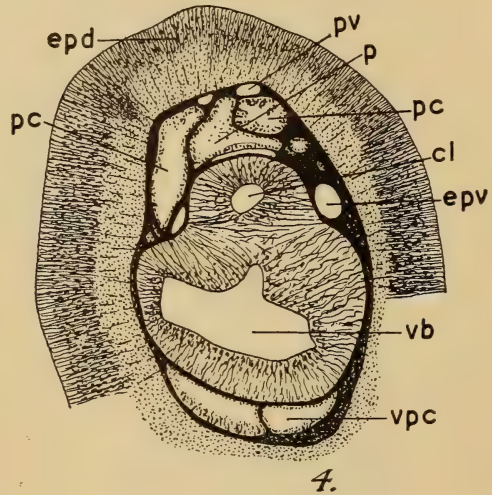


FIG. 4.—*Balanoglossus stephensoni*. Cross-section of the proboscis organs.  $\times 66$ . *cl*=central lumen of stomochord; *epd*=epidermis; *epv*=efferent proboscis vessel; *p*=pericardium; *pc*=right and left part of dorsal proboscis coelom; *pv*=proboscis vein; *vb*=ventral blind-sac of stomochord; *vpc*=ventral proboscis coelom.

In *B. stephensoni* I find the septum better developed. In front of it and free from it is seen the ventral proboscis artery; the septum itself begins a short distance behind the top of the stomochord, and from there it is complete and without a hole up to the posterior end of the ventral blind-sacs, that is near the frontal end of the skeleton (fig. 4). There are some smaller blood-vessels running through the septum. In contrast to *B. capensis* there are no dorso-ventral muscle fibres neither near the ventral artery nor at the sides of the septum, the latter being covered by a layer of coelomic epithelium only.

The dorsal part of the proboscis coelom is as usual divided into

right and left halves by the attachment of the pericardium to the basal membrane of the epidermis. According to von Bonde in one of his series the right dorsal proboscis coelom opens into the end-sac, and further by the proboscis pore to the exterior. This is unusual, as the right dorsal coelom nearly always splits up into smaller branches and ends blindly in the chondroid tissue, whereas the left opens to the exterior. This more usual condition was found by von Bonde in another specimen of *B. capensis*. In two series of sections of *B. capensis* which I studied the right coelomic sac was found to open to the exterior, the left splitting up in the chondroid tissue. It therefore seems that this is the normal condition in *B. capensis*, whereas in other Enteropneusta it is to be considered as abnormal. In *B. stephensoni* the normal condition obtains, the left dorsal proboscis coelom opening to the exterior. But in both species the ectodermal pouch or end-sac with which the coelom communicates and which in its turn opens to the exterior by the proboscis pore shows a bilateral symmetry, to some extent at least. It always extends in an anterior direction at one side, mostly the left, to its communication with the proboscis coelom. In both species, however, I found in addition an anteriorly directed extension of the end-sac on the opposite side, but in *B. capensis* it is on the left side and in *B. stephensoni* on the right side; in both species this extension ends blindly without communicating with the coelom. Hill sometimes found a similar condition in *B. australiensis*, and von Bonde describes this feature of the end-sac, called by him the proboscis canal, in one of his specimens. In between these two forward extensions of the end-sac lies the connection between the proboscis veins and the sinus venosus (fig. 5).

In both species the end-sac is large; in *B. capensis* it is nearly square in cross-section, in *B. stephensoni* it is greatly elongated dorso-ventrally (figs. 6 and 7). The proboscis pore of *B. capensis* is small and round and slightly inclined towards the left side. In *B. stephensoni* the pore is much larger and the end-sac extends for a short distance beyond the proboscis pore; a feature not found in *B. capensis*.

The stomochord of *B. capensis* is very compressed near its anterior end, as has been figured by von Bonde. In the sections, where the pericardium appears, the dorsal part of the stomochord disappears and the stomochord assumes the usual circular form in the cross-section (fig. 10). There are small isolated cavities in this anterior part, the continuous main lumen appearing only a short distance in front of the ventral extension of the stomochord. Although the

stomochord of *B. capensis* has the usual swelling or extension at its ventral side there is no blind-sac of the main lumen extending into

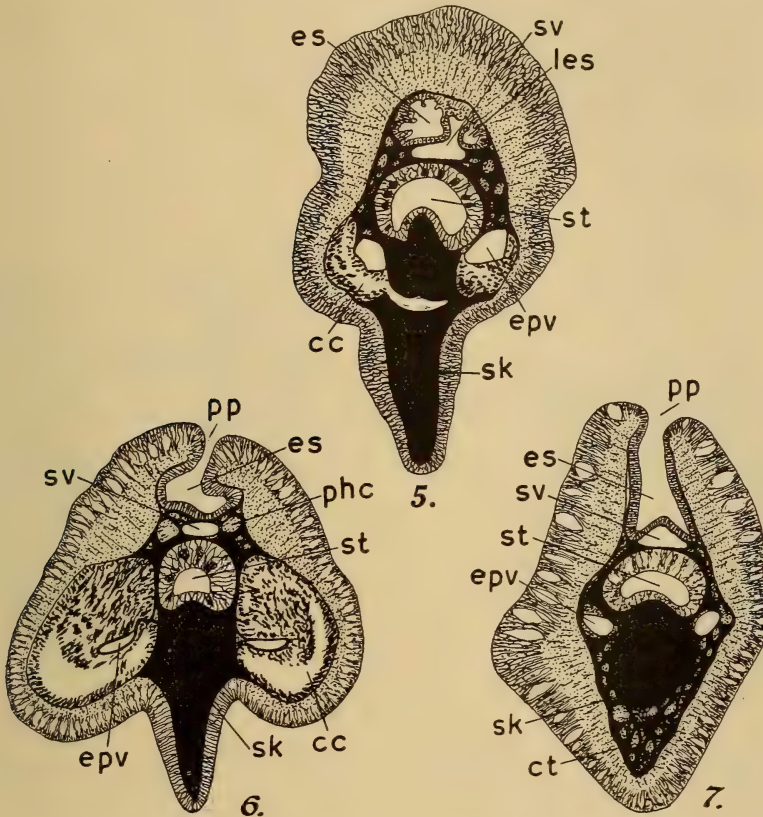


FIG. 5.—*Balanoglossus capensis*. Cross-section of the proboscis neck.  $\times 66$ . *cc*=collar coelom; *epv*=efferent proboscis vessel; *es*=end-sac; *les*=forward extension of end-sac at the left side; *sk*=skeleton; *st*=stomochord; *sv*=sinus venosus.

FIG. 6.—*Balanoglossus capensis*. Cross-section of the proboscis neck.  $\times 66$ . *cc*=collar coelom; *epv*=efferent proboscis vessel; *es*=end-sac; *phc*=top of periaemal cavity; *pp*=proboscis pore; *sk*=skeleton; *st*=stomochord; *sv*=sinus venosus.

FIG. 7.—*Balanoglossus stephensoni*. Cross-section of the proboscis neck.  $\times 66$ . *ct*=chondroid keel of skeleton; *epv*=efferent proboscis vessel; *es*=end-sac; *pp*=proboscis pore; *sk*=skeleton; *st*=stomochord; *sv*=sinus venosus.

this swelling, a feature also found by von Bonde. Instead of the one ventro-median blind-sac there are two ventro-lateral cavities. Usually, as in *B. australiensis* and *B. clavigerus*, these ventro-lateral

cavities communicate with a ventro-median extension of the main lumen. In *B. capensis*, however, they remain separate as there is no ventro-median extension (fig. 3). More towards the posterior end of the swelling, however, the cavities shift in dorso-lateral direction, where they have the appearance of dorso-lateral cavities of the stomochord (fig. 8), and at the level of the caudal end of the swelling

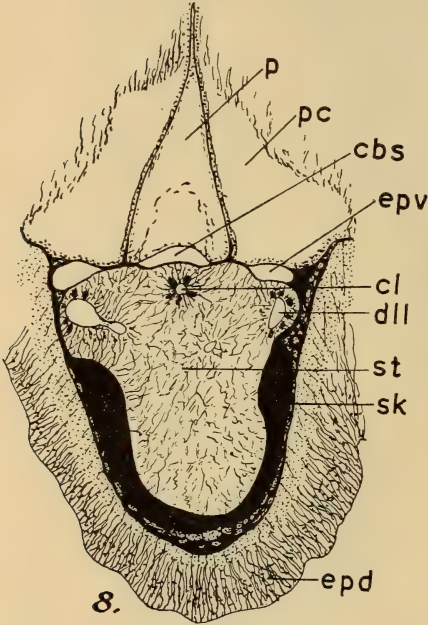


FIG. 8.—*Balanoglossus capensis*. Cross-section of the proboscis organs.  $\times 66$ . *cbs*=central blood space; *cl*=central lumen of stomochord; *dll*=dorso-lateral lumen of stomochord; *epd*=epidermis; *epv*=efferent proboscis vessel; *p*=pericardium; *pc*=dorsal proboscis coelom; *sk*=skeleton; *st*=stomochord.

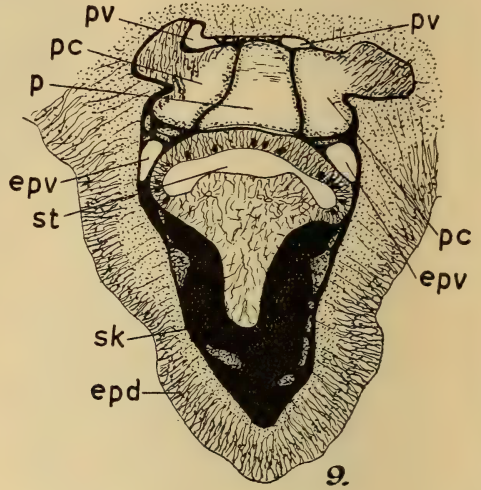


FIG. 9.—*Balanoglossus capensis*. Cross-section near the anterior end of the proboscis neck.  $\times 66$ . *epd*=epidermis; *epv*=efferent proboscis vessels; *p*=pericardium; *pc*=dorsal coelomic cavities of the proboscis; *pv*=proboscis veins; *sk*=skeleton; *st*=stomochord.

they communicate with the main lumen (fig. 9). In some species of *Balanoglossus* (*B. carnosus*, *B. biminiensis*, *B. jamaicensis*, *B. numeensis*, and *B. gigas*), which also in other respects are nearly related to each other, there are separate ventro-lateral and dorso-lateral cavities present in the stomochord; in others (*B. clavigerus*, *B. australiensis*, *B. stephensoni*) only the ventro-lateral cavities are found. *B. capensis* is intermediate between these groups, as the ventro- and dorso-lateral cavities intercommunicate on each side.

In *B. stephensoni* the anterior end of the stomochord is slightly compressed and contains some small isolated cavities. The con-



tinuous main lumen appears where the stomochord widens out in a ventral, and especially in a lateral, direction. At this place is found a large ventral blind-sac that is connected with the main lumen by a narrow canal (fig. 4). Where the ventral blind-sac disappears and the body of the stomochord passes over into the neck, the main central lumen widens out considerably. As in *B. capensis* the anterior part of the neck is nearly round in cross-section (fig. 6), then it becomes broader (fig. 7). Somewhat more towards the posterior end, where the proboscis neck has already fused with the collar, the dorsal wall of the stomochord of *B. stephensoni* bulges out in between the perihæmal cavities, which thereby are separated from each other ventrally (fig. 12). Furthermore the lumen of the stomochord sends out a blind-sac into this bulge. This may be a peculiarity of the specimen that was studied in serial sections, but it is more likely that this feature is of specific importance because a similar blind-sac is found in *B. misakiensis*. In *B. capensis* it is absent. As the crura of the skeleton spread out nearly in the transverse plane in *B. stephensoni*, the stomochord becomes very broad just before it communicates with the buccal cavity.

Anteriorly the skeleton starts in the cross-sections in the form of a U in both species, the anterior rim being of rather chondroid appearance in *B. capensis* (fig. 8). When the stomochord becomes smaller, owing to the disappearance of its ventral blind-sac, the skeleton becomes more of a solid structure (fig. 9) and the keel appears, which becomes more and more prominent until it soon surpasses the body in size. In *B. stephensoni* the anterior part of the keel is quite chondroid (fig. 7). In *B. capensis* the keel gradually diminishes in size towards its posterior end and disappears altogether a short distance in front of the splitting up of the body into the two crura. In *B. stephensoni*, on the other hand, the size of the keel is almost constant up to the region just in front of the splitting up of the body (fig. 12), and here the keel stops suddenly.

In some species of *Balanoglossus* (*B. biminiensis*, *B. carnosus*, *B. numeensis*) a reduction of the skeleton can be observed, caused by other tissues penetrating into the skeleton and more or less breaking it up. In *B. biminiensis* there is even a connection between the right and left collar coelomic cavities piercing through the body of the skeleton. Although the skeleton of *B. capensis* cannot be considered as being reduced, a similar connection between the collar coelomic cavities was found here, locally separating the keel from the body of the skeleton (fig. 5). Von Bonde also seems to have

observed this, as he mentions that the body, in the form of a rod, is completely separated from the keel.

In *B. capensis* the crura of the skeleton reach to about one-third of the length of the collar and they surround the buccal cavity for about one-third of its circumference. In *B. stephensoni* the crura are even shorter and are lying almost completely in the transverse plane.

The pericardium does not show any peculiarities in either species. In *B. stephensoni* its anterior end is at the same level as the top of the stomochord, and in *B. capensis* it is slightly behind this level, as was also observed by von Bonde.

In *B. stephensoni* the central blood space projects as a free blind-sac into the anterior part of the pericardium, as was described by Hill in *B. australiensis*. I do not consider this, however, to be of specific importance; it may be found in one specimen, and in another the blood space occupies its usual place in between the pericardium and the stomochord for the whole length of the pericardium. I was not able to find such a free projection of the blood space in *B. capensis*, but von Bonde describes it in the specimens of the species studied by him.

The glomerulus is markedly different in the two species. In *B. capensis* the glomerulus appears in the cross-sections at the same place as the stomochord, so that the glomerulus does not project in front of the stomochord. But the right and the left parts of the glomerulus are connected here along the dorsal side of the stomochord in front of the pericardium, and when later the pericardium appears in the sections this connection is found at the dorsal side of the pericardium (fig. 10). Thus the anterior part of the pericardium is completely covered by the glomerulus. More caudally the glomerulus is broken up into two lateral parts owing to the disappearance of the dorsal connection. Here the glomerulus covers the ventral half of the lateral pericardial wall and extends only slightly over the stomochord. Its caudal end is found near the anterior end of the ventral swelling of the stomochord.

In *B. stephensoni*, on the other hand, the glomerulus projects in front of both the stomochord and the pericardium, and it is already well developed when the top of the stomochord appears in the cross-sections. In this species the lateral parts of the glomerulus are connected along the ventral side of the stomochord and not along the dorsal side of the pericardium (fig. 11). When this ventral connection has disappeared from the sections the glomerulus almost

equally covers the pericardium and the stomochord. It disappears just in front of the ventral blind-sac of the stomochord. Although there is no dorsal connection of the two parts of the glomerulus there is a very small dorsal glomerulus at the side of the dorsal proboscis artery, quite isolated from the main glomerulus (fig. 11).

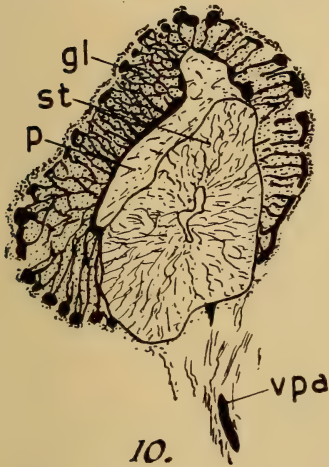


FIG. 10. — *Balanoglossus capensis*. Cross-section of the anterior part of the proboscis organs.  $\times 66$ . *gl* = glomerulus; *p* = pericardium; *st* = stomochord; *vpa* = ventral proboscis artery.

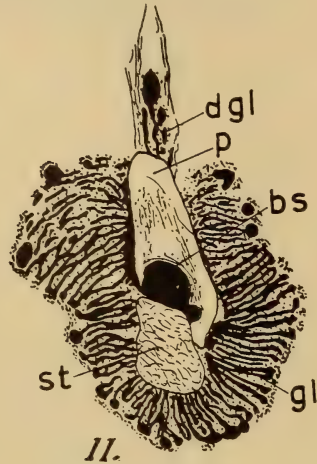
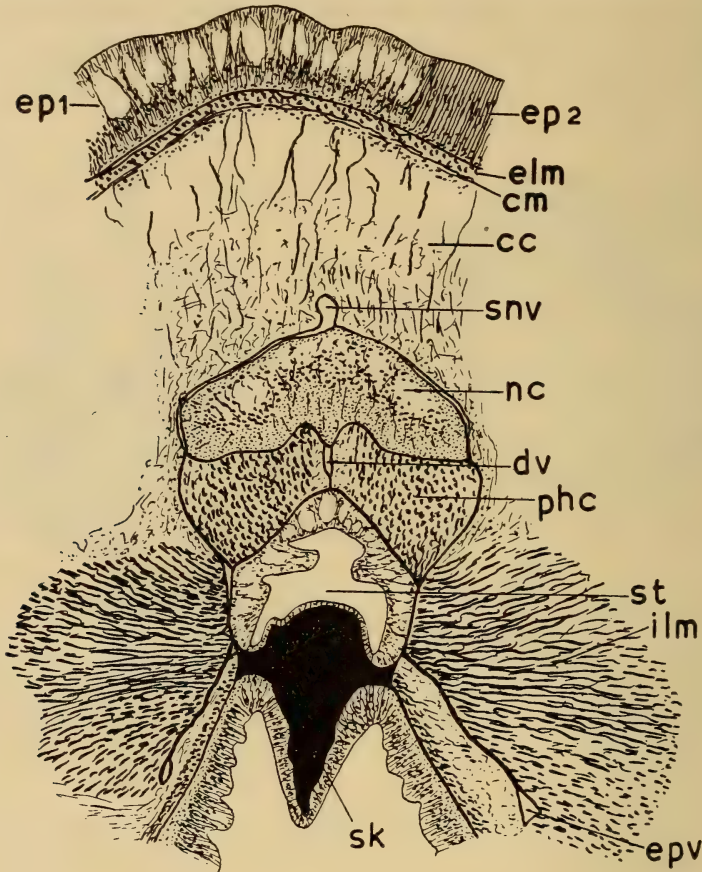


FIG. 11. — *Balanoglossus stephensoni*. Cross-section of the anterior part of the proboscis organs.  $\times 66$ . *bs* = central blood space; *dgl* = dorsal glomerulus; *gl* = glomerulus; *p* = pericardium; *st* = stomochord.

*Collar*.—In both species the epidermis of the collar shows the usual five zones, the second and fourth of which are composed of thin cells and stain more deeply, because the numerous slime glands occurring in the other zones are lacking in these two (fig. 12). The collar musculature also exhibits no features that might distinguish these species from others.

Concerning the coelom von Bonde writes that "the dorsal and ventral septa dividing the collar coelom into two halves are well developed." I find, however, that the ventral mesentery in both *B. capensis* and *B. stephensoni* is greatly reduced. It is only present in the most posterior part of the collar near the collar-trunk-septum. For nearly the whole length of the collar the right and left coelomic cavities communicate freely with each other along the ventral side. The dorsal septum is better developed. In *B. capensis* it begins

with the first and only dorsal nerve root and in *B. stephensoni* with the second root, from where it extends to the posterior end of the



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FIG. 12.—*Balanoglossus stephensoni*. Cross-section of the dorsal part of the collar near its anterior end.  $\times 66$ . *cc*=collar coelom; *cm*=circular musculature; *dv*=dorsal blood-vessel; *elm*=external longitudinal musculature; *epv*=efferent proboscis vessel; *ep1*=first epidermal zone; *ep2*=second epidermal zone; *ilm*=internal longitudinal musculature; *nc*=nerve cord; *phc*=perihæmal cavity; *sk*=skeleton; *snv*=supra-neural blood-vessel; *st*=stomochord.

collar. In *B. capensis*, however, there are some holes in this septum; in *B. stephensoni* it is entire.

The collar pores of both species exhibit the usual features. They have a longitudinal fold along their dorsal side, and the epithelium of this fold is hardly thinner than that of the ventral side of the pores.

The collar pores unite with the first branchial pouch near the external opening.

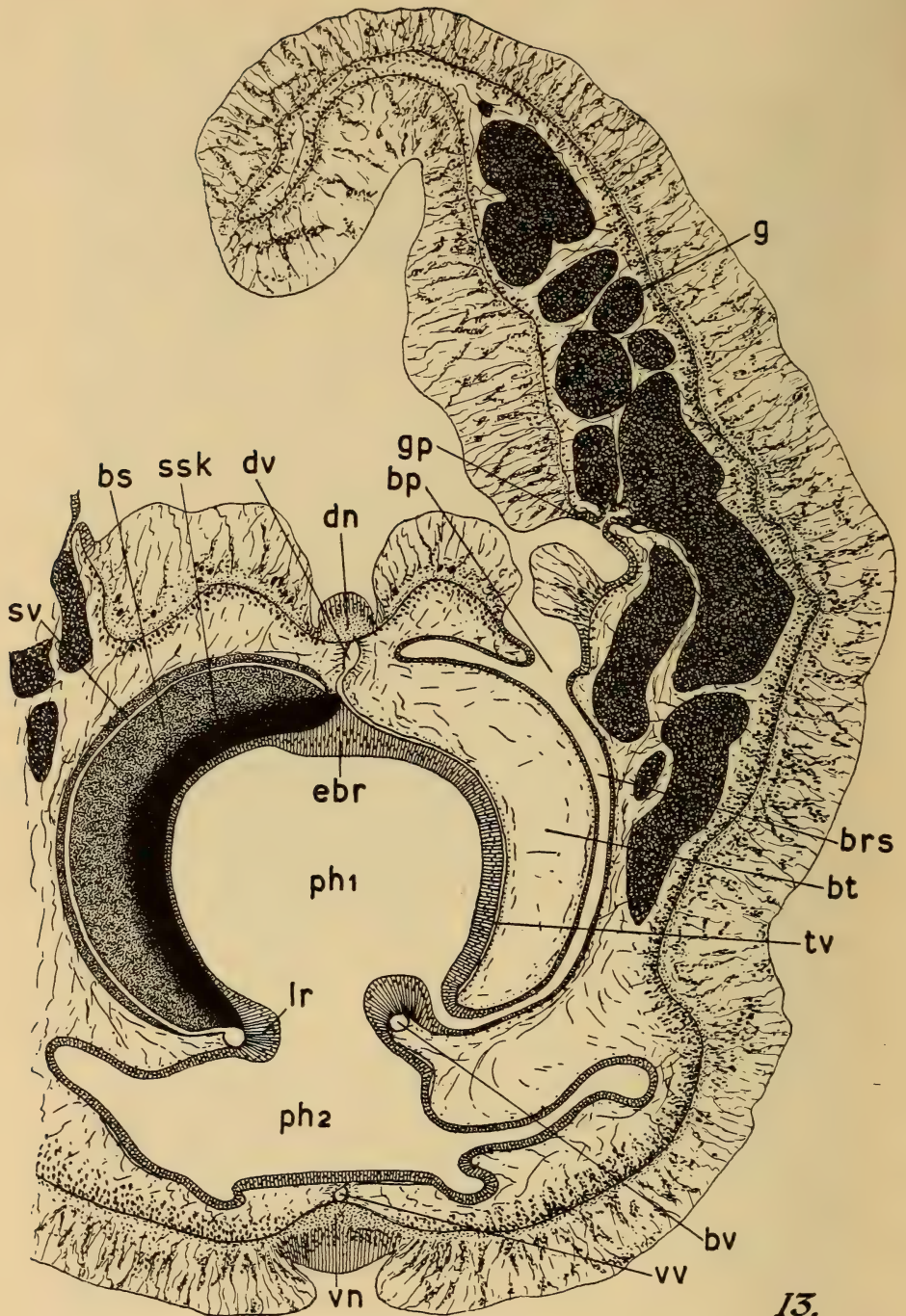
In *B. capensis* the anterior end of the perihæmal cavities is found at the level of the proboscis pore (fig. 6) and in *B. stephensoni* just behind this pore. In both species there are some openings in the septum separating the perihæmal cavities ventrally to the dorsal blood-vessel.

An anterior epidermal depression, connected with the anterior end of the collar nerve cord, is just indicated in *B. capensis*; in *B. stephensoni* it is entirely absent. In the latter species the posterior epidermal depression is also missing, whereas it is deep in *B. capensis*.

The collar nerve cord is very flattened in both species. There is neither an anterior nor a posterior neuropore, as the central canal is quite reduced to a number of small cavities. In *B. stephensoni* the lateral cavities are small and isolated; in *B. capensis* they have more the form of narrow elongated canals, of which a few occur behind each other throughout the whole length of the cord. This was also observed by von Bonde. A few isolated median cavities are found in both species. *B. stephensoni* has three dorsal nerve roots, the first of which runs free through the coelom as the dorsal mesentery only begins with the second root. All the roots are found in the anterior half of the collar. In *B. capensis* von Bonde found one root in one specimen and two roots in another. In the specimens I have studied there is a single root, but its peripheral part divides, so that it has two connections with the epidermis.

*Trunk*.—In all three specimens of *B. stephensoni* the epidermis of the trunk, and especially that of the branchial region, is very much swollen, except along the dorsal and ventral nerve cords and around the branchial and genital pores (fig. 13). As the intestine is quite empty, the animals apparently were kept for some time in a disk with sea-water before being fixed, and I have noticed in other species of *Balanoglossus* that the animals in these circumstances, unprotected as they are by stones or sand, secrete an enormous amount of slime.

*B. stephensoni* is characterised by its short and broad branchial tongues and septa; in *B. capensis*, as in other species of *Balanoglossus*, they are narrower. In *B. capensis* the dorsal or branchial part of the pharynx is larger than the ventral or digestive part, a feature also observed by von Bonde. This author, however, refers to this ventral part as the oesophagus, a term which is obviously inaccurate, for, as in *Amphioxus*, *Tunicates*, or *Vertebrates*, that part of the alimentary tract, which is pierced by the gill slits, is



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FIG. 13.—*Balanoglossus stephensoni*. Cross-section of the branchial region, composed from a number of sections.  $\times 45$ . *bp*=branchial pore; *brs*=branchial sac; *bs*=branchial septum; *bt*=branchial tongue; *bv*=parabranchial blood-vessel; *dn*=dorsal nerve cord; *dv*=dorsal blood-vessel; *ebr*=epibranchial ridge; *g*=gonad; *gp*=genital pore; *lr*=parabranchial or limiting ridge; *ph1*=branchial part of pharynx; *ph2*=digestive part of pharynx; *ssk*=septal skeletal bar; *sv*=septal blood-vessel; *tv*=tongue blood-vessel; *vn*=ventral nerve cord; *vv*=ventral blood-vessel.

termed the pharynx, and this is followed by the oesophagus, which in Enteropneusta extends up to the liver region. With the exception of Schizocardium the gill slits of Enteropneusta are confined to the dorsal part of the alimentary canal, for which reason the ventral half is best designated the digestive part of the pharynx. Taking into account the many folds of the ventral wall, the two parts of the pharynx are nearly equal in size in *B. stephensoni*.

As was to be expected in such a small animal, the number of gill slits in *B. stephensoni* is very small; I counted only 30 of them. Next comes *B. australiensis*, where, according to Hill, the number of gill slits does not exceed 40; in *B. capensis* there are 52, which also is a small number for a species of Balanoglossus. In both *B. capensis* and *B. stephensoni* the first gill slits open to the exterior by separate pores; in *B. misakiensis* the first four gills have a common opening. But *B. stephensoni* and *B. capensis* show a remarkable feature in connection with the first branchial pore. All these pores are found in a row at the medial side of the genital wings (fig. 13) as in other species of Balanoglossus, but the common opening of the collar canal and the first gill is found on the outer side of the genital wings (fig. 14). The wings, which are continuous with the dorsal wall of the collar, are only incipient in this region. The difference between the first and the second branchial pores is quite evident on comparing figs. 14 and 15. Even at the level of the second branchial pore the genital wings are better separated from the dorsal side of the body than they are at the first pore. In *B. australiensis* the first branchial pore also occupies a similar position on the outer side of the genital wing, though it is not mentioned in Hill's description. On the other hand, in *B. carnosus* and *B. biminiensis* the first branchial pore is on the medial side of the genital wing. I could not verify its position in the other species of Balanoglossus owing to lack of material.

The number of synapticula is 10 in *B. stephensoni* and 12 to 13 in *B. capensis*. Ventral blind pouches to the branchial sacs are absent in both species. In both species, owing to the fact that the epithelium on the inner side of the tongues attains about twice the thickness of that on the septa, the branchial tongues project slightly more into the pharyngeal cavity than the septa. Even so the epithelium of the tongues is rather low compared with that of other Enteropneusta. In both species the cells of the epibranchial ridge, and therefore also those of the inner side of the tongues and septa, are all of the same character.

The parabranchial ridges between the branchial and digestive parts of the pharynx are well pronounced in both species, and attain a thickness about twice that of the rest of the pharynx.

In *B. stephensoni* it could clearly be seen that a side branch of the parabranchial blood-vessel ascends along the peripheral edge of the

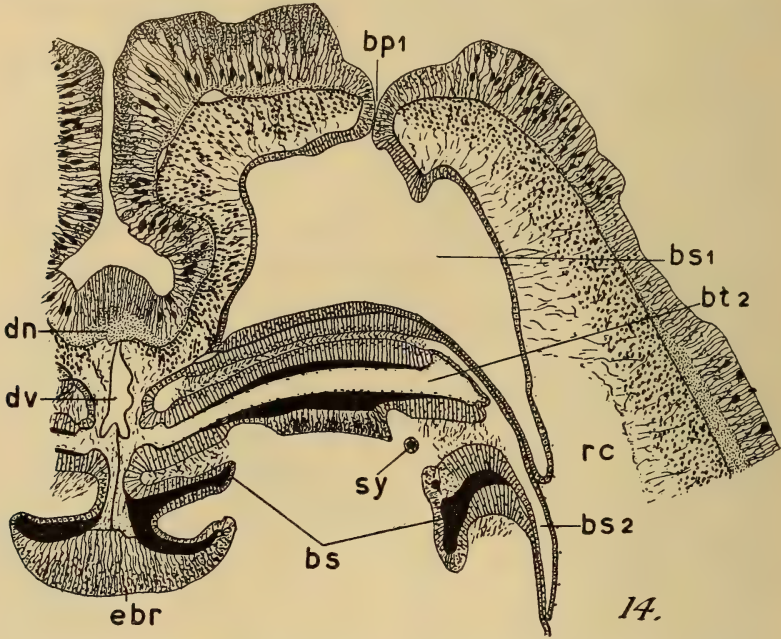


FIG. 14.—*Balanoglossus capensis*. Cross-section through the first branchial pore.  $\times 66$ . *bp1*=first branchial pore; *bs*=second branchial septum; *bs1*=first branchial sac; *bs2*=second branchial sac; *bt2*=second branchial tongue; *dn*=dorsal nerve cord; *dv*=dorsal blood-vessel; *ebr*=epibranchial ridge; *rc*=trunk coelom; *sy*=synapticulum.

branchial septum up to the dorsal end of the septum (figs. 13, 15). This vessel does not give off lateral branches, nor does it connect with the main dorsal vessel, but it breaks up into smaller vessels at the dorsal end of the septum. These smaller vessels could not be traced further; undoubtedly they enter the tongue and form a capillary network in the tongue, after which they unite again with another larger vessel that could be seen ascending just underneath the epithelium of the inner side of the tongue. This vessel joins the dorsal blood-vessel (fig. 13).

The post-branchial canal, forming a short continuation of the branchial part of the pharynx, is very similar in the two species.



The only difference is that in *B. stephensoni* the high epithelium of the post-branchial canal is divided into dorsal and lateral parts by two dorso-lateral grooves (fig. 16), whereas in *B. capensis* this epithelium is thrown into numerous irregular folds (fig. 17). In

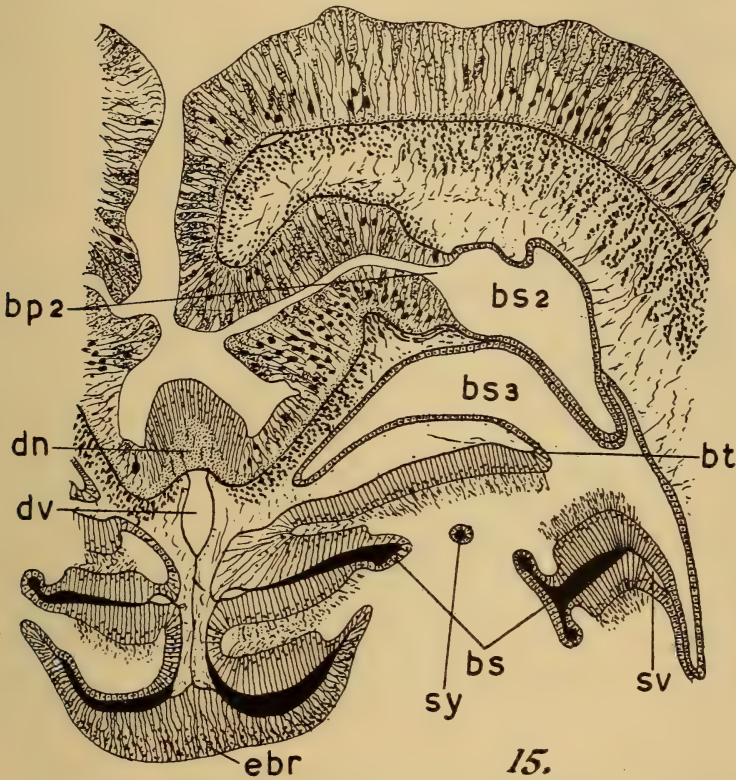


FIG. 15.—*Balanoglossus capensis*. Cross-section through the second branchial pore.  $\times 66$ . *bp2* = second branchial pore; *bs* = third branchial septum; *bs2* = second branchial sac; *bs3* = third branchial sac; *bt* = third branchial tongue; *dn* = dorsal nerve cord; *dv* = dorsal blood-vessel; *ebr* = epibranchial ridge; *sv* = septal blood-vessel; *sy* = synapticulum.

both species an anteriorly directed blind-sac of the canal, which in other species is found lying dorsally to the branchial part of the pharynx, is absent. Maser found that it may be absent in young individuals of *B. clavigerus* and *B. carnosus*, whereas it is present in older ones. The specimens of *B. stephensoni* and *B. capensis*, which I have studied, however, are not young individuals, as their gonads are fully developed. In both species the coelomic blind-pouches that usually project like a pair of valves into the oesophagus

are also absent. Otherwise these valves seem to be a constant character of the Ptychoderidae, though they are missing in *B. proterogonius* also. The post-branchial canal ends abruptly in both species.

In *B. stephensoni* the lateral septum could be followed for some considerable distance into the branchial region; it extends over 15 gill pores from the posterior end of the branchial region, *i.e.* about over half of that region. On the other hand, in the larger *B. capensis* it could only be followed for a distance of 10 gill slits, *i.e.* for not even one-fifth of the branchial region. As usual, the medial attachment of the branchial septum shifts along the last gill slit from the epidermis to the intestinal wall (figs. 16 and 17).

In *B. capensis* the first genital pore is found between the fourth and the fifth branchial pores, but the corresponding gonad is very small and it is either sterile or very young. All the anterior gonads are small, although they may contain some yolk cells. They occupy only a small part of the genital wing and hardly extend into the body proper. Posteriorly the gonads gradually increase in size, and although the tops of the gonads are also sterile they contain ripe eggs. This indicates that the row of gonads is about to extend in an anterior direction by the addition of secondary gonads. The gonads are profusely branched, and except for the top they fill up the whole of the genital wing; ventrally they extend into the body cavity and reach as far as the ventral end of the gills (fig. 17). Although the gonads are much more branched than in *B. clavigerus* they have only the primary pore in the sublateral line; secondary pores which may occur either at the distal or medial side of this line are absent.

Concerning the position of the most anterior of the gonads in *B. stephensoni*, these are even further forwards than in *B. proterogonius*, which was so called by Belichov on account of the occurrence of gonads between the second and third gills. In *B. stephensoni* gonads are found immediately behind the collar-trunk-septum; they can be seen in the same sections as the collar pores. These anterior gonads are small, but they show some branches and each opens by a separate pore in the niche between the genital wing and the body. Their pores are thus found in front of the second branchial pore. These pores may be considered as secondary ones unless it can be assumed that the sublateral line curves round in the niche. Further back in the row *B. stephensoni*, like *B. capensis*, has only primary pores in the sublateral line. Behind these anterior small gonads an

increase in size soon is observed, and the gonads become profusely branched in both dorsal and ventral directions. In *B. stephensoni* the peripheral part of the genital wing is quite empty; on the ventral side the gonads penetrate into the body cavity to about the middle of the gills (fig. 13).

As has been previously mentioned, a few of the liver saccules in

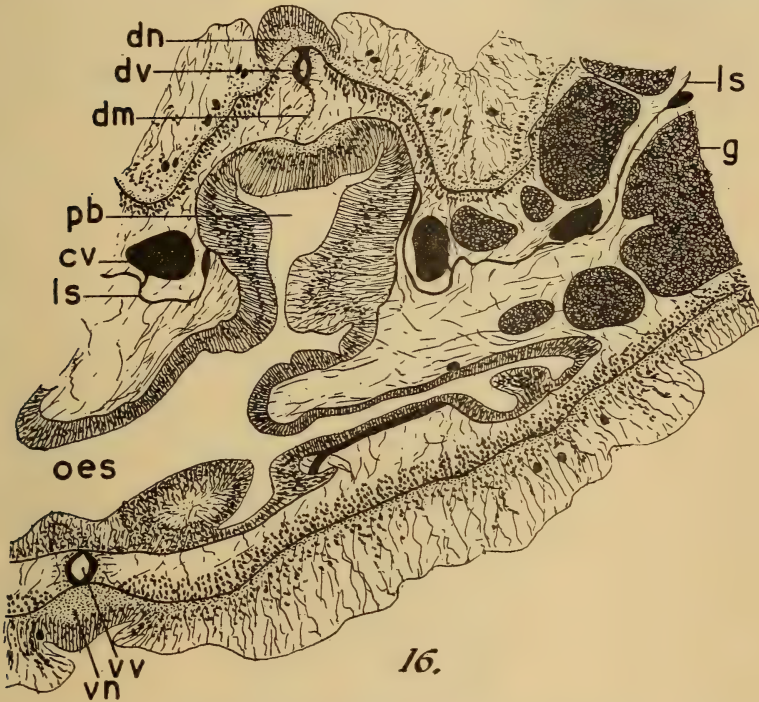


FIG. 16.—*Balanoglossus stephensoni* Cross-section at the level of the post-branchial canal.  $\times 45$ . *cv*=commissural blood-vessel; *dm*=dorsal mesentery; *dn*=dorsal nerve cord; *dv*=dorsal blood-vessel; *g*=gonad; *ls*=lateral septum; *oes*=oesophagus; *pb*=post-branchial canal; *vn*=ventral nerve cord; *vv*=ventral blood-vessel.

about the middle of the row are sharply defined by their dark colouration from the pure-white saccules in front of and behind them. In most Ptychoderidae all the anterior saccules differ from the posterior ones, sometimes, as in *B. biminiensis*, not only in colour but also in their form. In *B. carnosus* it was found that the two kinds of liver saccules were separated from each other by a well-pronounced swelling of the intestinal wall and the anterior saccules contain many glandular cells in their walls. In *B. stephensoni* the

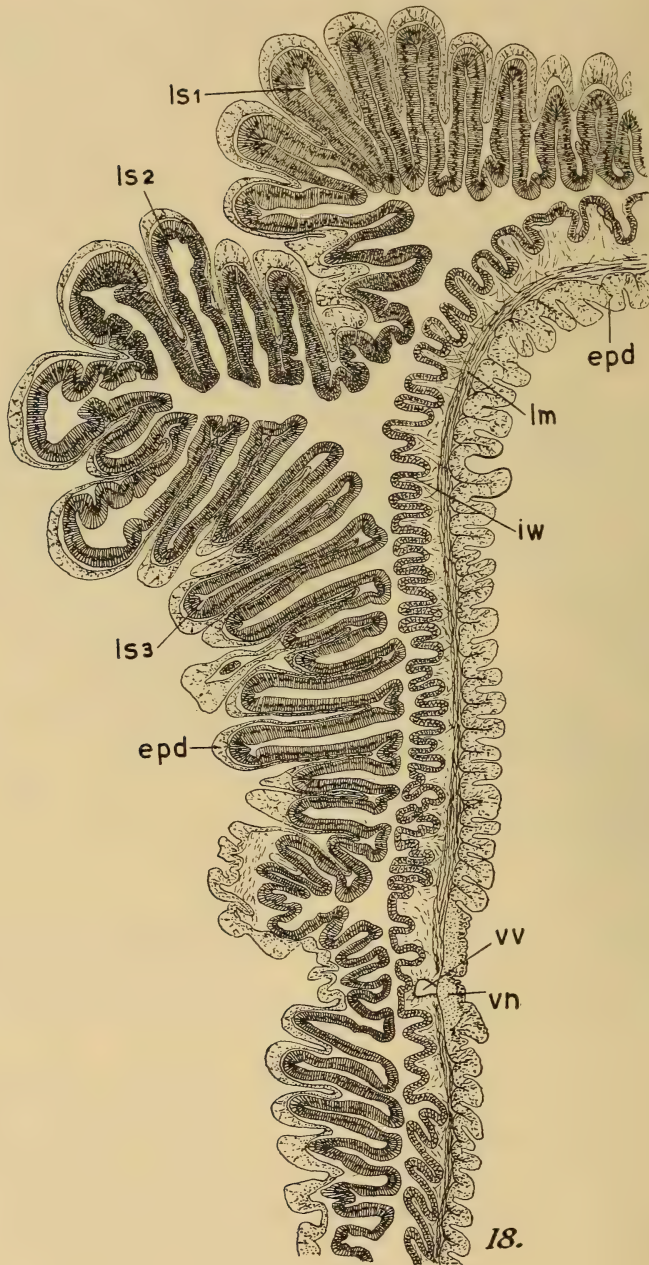


FIG. 18.—*Balanoglossus stephensoni*. Longitudinal section of the hepatic region.  $\times 27$ . *epd*=epidermis; *iw*=ventral wall of intestine; *lm*=longitudinal musculature; *ls1*, *ls2*, and *ls3*=first, second, and third region of liver saccules; *vn*=ventral nerve cord; *vv*=ventral blood-vessel.



FIG. 17.—*Balanoglossus capensis*. Cross-section at the level of the post-branchial canal.  $\times 45$ . *cv*=commissural blood-vessel; *dn*=dorsal nerve cord; *dv*=dorsal blood-vessel; *gp*=genital pore; *ls*=lateral septum; *lv*=lateral blood-vessel; *oes*=oesophagus; *pb*=post-branchial canal; *vn*=ventral nerve cord; *vv*=ventral blood-vessel.

FIG. 19.—*Balanoglossus stephensoni*. Cross-section of the pygochord.  $\times 290$ . *iw*=intestinal wall; *pg*=pygochord; *vv*=ventral blood-vessel.

dark saccules could easily be identified in sections by numerous small dark granules in the liver cells. The nuclei of the liver cells occupy their usual position almost in the middle of the cell and the dark granules are found only at the side of the nucleus facing the intestinal lumen (fig. 18). Although there is a clear limit between the saccules with granular cells and those without, a swelling of the intestinal wall such as occurs in *B. carnosus* could not be found. All the saccules have the same form. At the anterior as well as at the posterior end of the row a few small saccules are found that do not cause an epidermal bulging, so that they are invisible from the outside. The ventral wall of the intestine in the liver region is thrown into numerous small transverse folds. As the epidermis in this region also shows similar folds, these may have been caused, at least partially, by the contraction of the ventral longitudinal muscles during fixation.

The intestine in the abdominal region of *B. stephensoni* has the usual pair of ciliary bands, but I was unable to find a continuous line of epidermis without glandular cells, corresponding to the ciliary bands as described by Hill in *B. australiensis*, although indications of it were seen here and there. Anteriorly the ciliary bands could be followed through the whole liver region, but at the anterior end of this region they become very indistinct and they do not extend in front of it; in *B. australiensis*, however, they extend for a considerable distance into the genital region. Posteriorly the ciliary bands stop at the caudal region.

The anus is surrounded by a feebly developed sphincter.

The pygochord of *B. stephensoni* extends over the whole length of the caudal region, and it is not separated from the intestinal wall. Anteriorly it starts as a small evagination of the wall of the intestine in the ventral midline. Growing larger it reaches the ventral blood-vessel, and more posteriorly, where this vessel ends, it comes into contact with the basal membrane of the epidermis (fig. 19). The pygochord has the same breadth throughout. Its cells, especially those along the dorsal side near the intestine, contain large vacuoles.

#### *Diagnosis of Balanoglossus capensis* (Gilchrist).

Total length up to 13 cm.; in a specimen of 13 cm. the length of the proboscis is 3.5 mm., that of the collar 3 mm., of the branchial region 7.5 mm., the total length of the genital wings is 37 mm. and of the liver region 35 mm.; the abdominal region is 68 mm. long. Genital wings fused with posterior rim of collar; they reach

their maximum breadth at the end of the branchial region, from where they gradually decrease in size; they reach well into the liver region, where they fade away gradually. The liver saccules form a regular row of about 75 visible saccules on each side. The middle liver saccules are dark, the anterior and posterior ones light in colour.

Right and left halves of the glomerulus connected along the dorsal side of the pericardium; glomerulus only slightly covering the stomochord; ventral proboscis septum greatly reduced but extending to the end of the ventral coelomic blind-sacs; stomochord without ventro-median blind-sac, but with ventro-lateral blind-sacs which communicate with dorso-lateral blind-sacs; only the latter are in connection with the central lumen. Keel of skeleton well developed, gradually diminishing in size towards its posterior end; crura short, surrounding the buccal cavity for about one-third of its circumference. In the majority the right dorsal coelomic cavity of the proboscis opens into a large end-sac, which has a blind forward extension on the left side as well. Proboscis pore small and round.

Nerve cord without central lumen, with one or two dorsal nerve roots. Ventral collar mesentery only present near hind end of collar.

Anterior branchial sacs not connected with each other, each opens to the exterior by a separate pore; first branchial pore at the outer side of the genital wings, all the others at the medial side. Branchial sacs without ventral blind-sacs. 12 to 13 synapticula, about 50 gills. Post-branchial canal without anteriorly directed blind-sac; no valves projecting into the oesophagus. The first genital pore between the 4th and the 5th branchial pores; except near the anterior end of the row the gonads are large and much branched; no secondary genital pores.

*Locality.*—False Bay, South Africa.

*Diagnosis of Balanoglossus stephensoni* n. sp.

Total length up to 4 cm.; in a specimen with a length of 38 mm. the proboscis is 1.5 mm. long, the collar nearly 2 mm., the branchial region 3 mm.; the total length of the genital wings is 12.5 mm.; the abdominal region is 20 mm. long. Genital wings fused with posterior rim of the collar; they reach their maximum breadth near the hind end of the branchial region, this breadth remaining practically constant up to the beginning of the liver region. In the anterior part of the liver region the genital wings decrease abruptly in size. The short liver region begins and ends abruptly. The

liver saccules form a regular row on each side and there are about 20 saccules visible in each row. The middle liver saccules are dark, those in front and behind light in colour.

Anteriorly the right and left halves of the glomerulus are connected with each other along the ventral side of the stomochord. Glomerulus covering the pericardium and the stomochord about equally. There is a very small dorsal glomerulus present. Ventral proboscis septum extends from shortly behind the top of the stomochord to the end of the ventral coelomic blind-sacs. Stomochord with large ventro-median blind-sac, which communicates with the central lumen; no dorso-lateral blind-sacs. Keel of the skeleton well developed, its size is almost constant throughout its whole length; it stops suddenly just in front of the bifurcation of the body into the crura. Crura of skeleton short, situated nearly in the transverse plane. The left dorsal coelomic cavity of the proboscis opens into a large end-sac, which has a blind forward extension on the right side as well. Proboscis pore large and elongated.

Nerve cord without central lumen, with three dorsal nerve roots. Ventral collar mesentery only present near the hind end of the collar.

Each anterior branchial sac opens to the exterior by a separate pore; first branchial pore at the outer side of the genital wings, all the others at the medial side. Branchial sacs without ventral blind-sacs. 10 synapticula, about 30 gills. Post-branchial canal without anteriorly directed blind-sac; no valves projecting into the oesophagus. The first genital pore between the first and second branchial pores. Gonads large and much branched; no secondary genital pores.

*Locality.*—Port Elizabeth, South Africa.

Type in South African Museum, Cape Town.

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